

Crop Size and Fruit Neighborhood Effects on Bird Visitation to Fruiting *Schefflera morototoni* Trees in Puerto Rico¹

James F. Saracco², Jaime A. Collazo, Martha J. Groom³, and Tomás A. Carlo⁴

North Carolina Cooperative Fish and Wildlife Research Unit, Biological Resources Division, U. S. Geological Survey, Department of Zoology, North Carolina State University, Raleigh, North Carolina 27695-7617, U.S.A.

ABSTRACT

Studies of zoochorous seed dispersal systems often consider crop size, yet seldom consider the kinds and amounts of fruits surrounding parent plants (the fruit neighborhood) when attempting to explain among-plant variation in fruit removal. We studied avian frugivory at 24 *Schefflera morototoni* trees from February to May 1998 in central Puerto Rico. The number of fruits removed by avian seed dispersers per visit was similar among focal trees (typically 2–4). In contrast, visitation rate was highly variable (range: 0–71 visits per 4 h). We used multiple regression analyses to evaluate the relative roles of crop size (focal tree ripe fruit abundance) and fruit neighborhood variables (measured within 30 m of focal trees) in affecting visitation to focal trees by avian frugivores. Visitation rate was positively related to crop size (although this variable was only significant in one of four regression models considered) and negatively related to the presence or abundance of conspecific fruits, suggesting that trees competed intraspecifically for dispersers. Relationships between visitation and heterospecific fruits were mixed—some kinds of fruits appeared to enhance visitation to focal trees, while others seemed to reduce visitation. In most regression models, neighborhood variables had larger effects on visitation than focal tree fruit crop size. Our results highlight the important effects of local fruiting environments on the ability of individual plants to attract seed dispersers.

RESUMEN

Los estudios de sistemas dispersadores de semillas zoocoras por lo general consideran el tamaño de la cosecha, sin embargo, raras veces consideran los tipos y cantidades de frutos en los alrededores de las plantas madres (las frutas del vecindario) cuando intentan explicar entre plantas, la variación de extracción de frutos. Nosotros estudiamos la frugivoria de aves en 24 árboles de *Schefflera morototoni* entre Febrero y Marzo de 1998 en la parte central de Puerto Rico. El número de frutos removidos en cada visita por las aves dispersadoras de semillas fue similar entre los árboles focales (típicamente de 2 a 4). En contraste, la proporción de visitas fue muy variable (intervalo = 0–71 visitas cada 4 horas). Nosotros utilizamos análisis de regresión múltiple para evaluar el rol relativo del tamaño de la cosecha (árboles focales con abundancia de frutos maduros) y variables en frutos del vecindario (medidos dentro de los 30 m de los árboles focales) en el efecto de visitas por aves frugívoras a los árboles focales. La proporción de visitas estuvo positivamente relacionado con el tamaño de la cosecha (aunque esta variable fue solamente significativa en uno de los cuatro modelos considerados) y negativamente relacionado a la presencia y a la abundancia de frutos coespecíficos, sugiriendo que los árboles compitieron intraespecíficamente por los dispersores. Las relaciones entre visitas y frutos heteroespecíficos fue mixta—algunos tipos de frutos parecen promover las visitas a los árboles focales, mientras que otros parecen reducir las visitas. En la mayoría de los modelos de regresión, las variables de “vecindario” tuvieron un mayor efecto sobre las visitas que en el tamaño de la cosecha de frutos del árbol focal. Nuestros hallazgos enfatizan la importancia que pueden tener los efectos de los ambientes locales de frutos en la habilidad de plantas individuales en atraer dispersadores de semillas.

Key words: frugivory; plant–animal interactions; seed dispersal; *Spindalis portoricensis*; shade coffee plantation; tropical forest.

MANY PLANT SPECIES PRODUCE FLESHY OR ARILLATE FRUITS that are dispersed by animals (Howe & Smallwood 1982). Identifying factors that influence plant choice by frugivores is a critical step in linking frugivore behavior and plant demography, and thus in understanding how animals affect the distribution, abundance, and evolution of plant mutualists (Schupp 1993). Most studies attempting to make this link have focused on characteristics of parent plants (*i.e.*, fruit quality or quantity). In controlled aviary experiments, frugivorous birds often discriminate among fruits that vary in aspects of fruit quality, such as color, nutrients, or accessibility (*e.g.*, Moermond & Denslow 1983, Johnson *et al.* 1985, Stiles 1993, Siitari *et al.* 1999, Schaefer *et al.* 2003). Such selectivity has proven difficult to show in the field, where the only plant characteristic

that consistently explains large proportions of among-plant variation in fruit removal is fruit quantity (*i.e.*, crop size; Davidar & Morton 1986, Denslow 1987, French *et al.* 1992, Willson & Whelan 1993, Alcántara *et al.* 1997, Jordano & Schupp 2000). Nevertheless, frugivore responses to crop size can be highly variable over space and time (*e.g.*, Sallabanks & Courtney 1993, Ortiz-Pulido & Rico-Gray 2000). Much of the spatial and temporal variation in visitation and fruit removal rates among plants could be due to factors external to parent plants, yet these variables are seldom considered.

Among the most likely external variables to influence avian foraging are the kinds and amounts of fruits available to frugivores within some area surrounding parent plants (the “fruit neighborhood”; Herrera 1986). A number of studies have shown fruit removal rates at individual plants to be negatively related to the presence or abundance of nearby conspecific (Moore & Willson 1982, Manasse & Howe 1983, Denslow 1987; but see French *et al.* 1992) or heterospecific (Herrera 1984) fruits. Nevertheless, a plant’s ability to attract seed dispersers could also be enhanced by the presence of nearby fruiting trees if these neighbors attract frugivores to areas that might not otherwise be visited (Sargent 1990, García *et al.* 2001, van Ommeren & Whitham 2002). Such facilitative interactions

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² Current addresses: The Institute for Bird Populations, P.O. Box 1346, Pt. Reyes Station, CA 94956 U.S.A., and Biology Program, University of Alaska Southeast, 11120 Glacier Highway, Juneau, AK 99801, U.S.A.; e-mail: jfsaracc@gustavus.ak.us

³ Current addresses: Interdisciplinary Arts and Sciences, University of Washington, Bothell, WA 98021-4900, U.S.A., and Department of Biology, University of Washington, Seattle, WA 98195-1800, U.S.A.

⁴ Current address: Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309-0334, U.S.A.

between plants could be particularly prevalent on small spatial scales or where fruit is especially scarce or patchily distributed (Rathcke 1983).

In this paper, we describe interactions between avian frugivores and fruiting plants during a single fruiting season in central Puerto Rico. For the most commonly consumed plant species, *Schefflera morototoni*, we use multiple regression models to assess variation in bird visitation rates to individual fruiting trees as a function of crop size (ripe fruit abundance) and the presence or abundance of nearby ripe conspecific and heterospecific fruits. We expected visitation rates to be most strongly influenced by intraspecific interactions among plants (Howe & Estabrook 1977); that is, by crop size and conspecific neighborhood fruits. Furthermore, assuming that seed-dispersing frugivores were a limiting resource to fruiting trees, we expected these intraspecific interactions to be competitive. Because heterospecific fruits were less abundant and less commonly consumed by avian frugivores, we expected them to be of lesser importance in explaining focal tree visitation rates. Furthermore, it has been suggested that many bird-consumed fruits may be complementary resources (Whelan *et al.* 1998). Thus, we expected interactions between focal trees and at least some heterospecific fruit taxa would be facilitative in nature.

METHODS

STUDY AREA.—This study was conducted at a lower montane site of approximately 80 ha in central Puerto Rico (18°14'N, 66°31'W; elev. 625–710 m). The habitat was a mosaic of moist secondary subtropical forest (Ewel & Whitmore 1973) and shaded coffee plantation. Common trees were coffee shade species such as *Inga vera*, *Inga laurina*, *Andira inermis*, and *Guarea guidonia*, and trees typical of lower montane secondary forests such as *Schefflera morototoni*, *Cecropia schreberiana*, *Miconia* spp., *Alchornea latifolia*, Lauraceae spp., *Casearia* spp., and *Cordia sulcata* (plant nomenclature follows Liogier & Martorell 2000).

Common fruit-eating birds included Puerto Rican Stripe-headed Tanager (*Spindalis portoricensis*), Puerto Rican Tanager (*Nesospingus speculiferus*), Antillean Euphonia (*Euphonia musica*), Puerto Rican Bullfinch (*Loxigilla portoricensis*), Black-whiskered Vireo (*Vireo altiloquus*), Pearly-eyed Thrasher, (*Margarops fuscatus*), Red-legged Thrush (*Turdus plumbeus*), Scaly-naped Pigeon (*Columba squamosa*), and Puerto Rican Woodpecker (*Melanerpes portoricensis*; bird nomenclature follows Raffaele *et al.* 1998). Common consumers of *S. morototoni* fruits in the study area employed seed handling techniques that are consistent with seed dispersal, and undamaged seeds recovered from fecal samples further support this assertion (Carlo 1999, Carlo *et al.* 2003). Two infrequent *S. morototoni* consumers, *C. squamosa* and *L. portoricensis*, may damage seeds during mandibulation or gut passage (Moermond & Denslow 1985); however, we lack the data necessary to critically evaluate this possibility.

FOCAL TREE SPECIES.—*S. morototoni* is widely distributed in the humid Neotropics (Liogier 1995). It is a pioneer species typical of disturbed forests and gaps (Crow 1980, Denslow 1980). In Puerto Rico, it occurs in montane forests at middle elevations, particularly on steep slopes, and less commonly at lower elevations in the northern coastal limestone hills (Little & Woodbury 1976). Adults in the study area averaged 30.0 cm dbh ($N = 225$) and 16 m in height.

S. morototoni fruits are 2-seeded drupes (4–6 mm long, 6–10 mm broad) borne on 20–60 cm compound panicles (Liogier 1995). The pulp is relatively rich in lipids and proteins (Snow 1971, Herrera 1981). Crop sizes observed during the study averaged about 68,000 fruits; the largest tree contained an estimated 1,000,000 fruits (estimation method described below in “Crop size and neighborhood measurements”). It was the most abundant fruit in the study area (Carlo *et al.* 2003). Fruits ripen in almost every month in Puerto Rico. During 1998, ripe fruits were primarily available between February and June on the study area, peaking in abundance between March and April.

PLOT-LEVEL FORAGING OBSERVATIONS.—To identify plant species likely to influence bird visitation to *S. morototoni* trees, we conducted foraging observations within a centrally located 8.28 ha grid between 2 February and 18 May 1998 (data are a subset of those reported in Carlo *et al.* 2003). On 6–7 days each month, one observer traversed the grid for approximately 5 h, beginning about 1 h after sunrise. On each observation day, the observer commenced searching for foraging birds from a random starting point. Movement from the starting point was guided by visual and auditory cues of seven fruit-eating bird species: *S. portoricensis*, *N. speculiferus*, *E. musica*, *L. portoricensis*, *V. altiloquus*, *M. fuscatus*, and *T. plumbeus*. All observations of frugivory were noted by recording the bird and plant species involved. We did not make sequential foraging observations (*i.e.*, only one fruit species was recorded for an individual bird) in order to reduce statistical problems associated with serially autocorrelated data (Hejl *et al.* 1990).

FOCAL TREE OBSERVATIONS.—We randomly selected 24 *S. morototoni* focal trees between 2 February and 3 May 1998 with the constraints that (1) the entire canopy had to be visible from a nearby vantage point and (2) the tree had to be located >70 m from another focal tree (to increase the likelihood of statistical independence). Each focal tree was observed for 4 h (usually on a single day) between 0630 and 1300 AST. All birds entering focal trees were noted and identified to species with the aid of binoculars. For frugivorous bird species, we recorded the number of visits made to each tree. We defined a “visit” to be any instance of a bird entering a part of the tree with ripe fruit and staying for a period consistent with fruit consumption. Whenever birds could be observed feeding for the entire visit, we recorded the number of fruits that were consumed.

CROP SIZE AND NEIGHBORHOOD MEASUREMENTS.—On focal tree observation days, we estimated the number of ripe and unripe fruits on focal trees by counting fruits on portions of infructescences (using binoculars) and extrapolating for the remainder of the tree. We considered grayish-purple fruits that were round in shape to be ripe. We seldom observed birds eating thinner green fruits. Because *S. morototoni* produce very large crops of small fruits, estimates were calibrated by complete counts of fruits on infructescences that had fallen to the ground. Prior to the analyses, ripe fruit abundance estimates were categorized using an index (hereafter FAI) that essentially followed a log₂ scale (0 = no ripe, 1 = 1–16 ripe, 2 = 17–32 ripe, 3 = 33–64 ripe, . . . , 16 = 262,145–524,288, 17 = >524,288).

For each focal plant, we measured the distance and direction to all other plants bearing fruit within 30 m (2827 m²). This was the largest

area that could consistently be mapped by a single observer within 1 week of the observation day; it is consistent with the spatial scale at which avian frugivores appear to perceive fruit patches (Saracco *et al.* 2004). All fruiting plants in these “neighborhoods” were identified to species, although some were identified to genera whenever species-level identification was uncertain. Of the species lumped at the generic-level, *Phoradendron* (Viscaceae) mistletoes were particularly common. We have since identified two species that probably comprised all of the *Phoradendron* spp. encountered during this study: *P. racemosum*, which has yellow fruits and grew primarily on *Inga vera* trees, and *P. hexastichum*, which has white fruits and grew primarily on *Cecropia schreberiana* trees (T. A. Carlo & J. E. Aukema, unpubl. data). For all fruiting plants encountered in neighborhoods, ripe fruit abundance was estimated (as described above for focal trees), with the exception that we counted fruits directly for plants with few fruits and canopies entirely visible from the ground. Prior to analyses, we summed the estimated ripe fruit abundance across individuals for each species (or genera for less frequently encountered species) and assigned a score from the FAI described above for focal trees.

STATISTICAL ANALYSES.—We summarized among-plant variation in two measures of seed removal success: (1) visitation rate and (2) the number of fruits consumed per visit (Schupp 1993). We used multiple regression to assess the contribution of crop size and neighborhood variables in explaining focal tree visitation rate. We examined two response variables and two sets of explanatory variables. Response variables were: (1) the number of visits by *S. portoricensis* (the most frequent visitor to *S. morototoni* trees) and (2) the number of visits by all species. Both were square root (+0.5) transformed in order to meet normality, linearity, and homoscedasticity assumptions (Chatterjee *et al.* 2000). We considered two distinct sets of explanatory variables. The first set included the focal tree FAI and the FAIs of fruit taxa (species or genera) occurring in neighborhoods. We only considered fruit taxa that occurred in ≥ 5 neighborhoods and were observed to be eaten by birds on ≥ 5 occasions during plot-level frugivory observations. The second set of explanatory variables also included the focal tree FAI, but rather than using FAIs for neighborhood fruit taxa, we used indicator variables denoting their presence-absence (P-A). By considering P-A, we not only addressed a slightly different biological hypothesis (effect of presence vs. abundance) but also increased our ability (*i.e.*, our statistical power) to detect important patterns for strongly right-skewed taxa that had many zeros. P-A variables were also statistically attractive because outliers had less influence on regression results. We standardized explanatory variables to mean zero and unit variance to facilitate comparison of the relative importance of FAI and P-A variables.

We selected models for each response and set of explanatory variables using backward stepwise selection with probability to remove a variable = 0.10. Plots of predicted values \times residuals, explanatory variables \times residuals, and index plots of Cook’s Distances were examined to check for violations of model assumptions and outliers (Chatterjee *et al.* 2000). No gross violations of model assumptions were evident. Because focal trees were sampled sequentially throughout the season, we examined plots of residuals from the selected models \times day of year. These plots, as well as Durbin-Watson tests suggested there were no significant temporal patterns remaining in the data after model fitting. All analyses

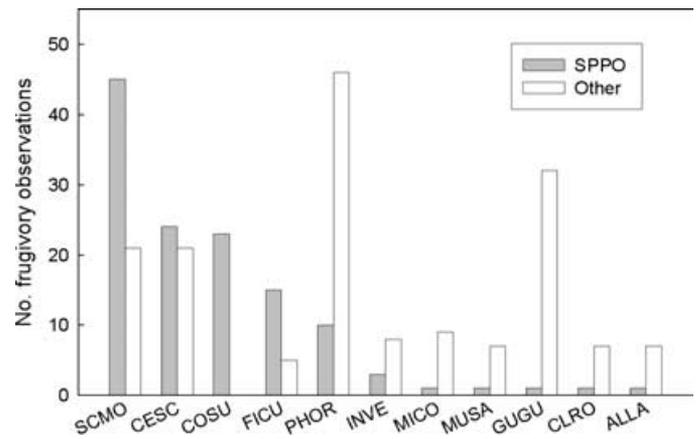


FIGURE 1. Plot-level frugivory by *Spindalis portoricensis* (SPPO) and for all other species on the study area in central Puerto Rico 2 Feb–18 May 1998. Consumption of an additional 14 plant species was recorded less frequently (< 5 observations). Species codes are: *Schefflera morototoni* (SCMO), *Cecropia schreberiana* (CESC), *Cordia sulcata* (COSU), *Ficus* spp. (FICU), *Phoradendron* spp. (PHOR), *Inga vera* (INVE), *Miconia* spp. (MICO), *Musa* spp. (MUSA), *Guarea guidonia* (GUGU), *Clusia rosea* (CLRO), *Alchornea latifolia* (ALLA).

were conducted using JMP for Windows Ver. 5.0 (SAS Institute, Inc., Cary, NC).

RESULTS

PLOT-LEVEL FRUGIVORY.—We recorded 24 fruit taxa consumed by avian frugivores during the study. Foraging observations suggested that *S. morototoni* was the most commonly consumed fruit (Fig. 1); it was particularly important in the diet of *Spindalis portoricensis* (Table 1). Fruit diet overlap between *S. portoricensis* and the other fruit consumers was considerable; however, some fruits seemed to be exploited chiefly by *S. portoricensis* (*e.g.*, *Cordia sulcata*), while others were primarily consumed by other frugivores (*e.g.*, *Guarea guidonia* was mostly eaten by *Vireo altiloquus* and *Loxigilla portoricensis*; Carlo *et al.* 2003).

FOCAL TREE VISITATION.—Visitation rates at focal trees ranged from 0 to 71 visits per 4 h (for all bird species). Eighty-six percent of visits were by *S. portoricensis* (Table 1). We could only determine with certainty that fruit was consumed on 58 percent of bird visits to focal trees. Nevertheless, the locations of birds in trees and the amount of time spent there suggested that fruit was probably consumed on most visits. The number of fruits consumed per visit, based on a sample of 38% of focal tree visits, suggested that most visits resulted in few fruits (and seeds) removed (median = 3 fruits, quartiles = 2, 4; $N = 170$ observations). The amount of fruit consumed per visit was similar for *S. portoricensis* and other bird species ($t = 0.83$, $df = 168$, $P = 0.93$).

CROP SIZE AND NEIGHBORHOOD EFFECTS ON VISITATION.—We considered all heterospecific fruit taxa shown in Figure 1 for inclusion in multiple regression models except *Ficus* spp., *Musa* spp., *Clusia rosea*, and

TABLE 1. Avian frugivore use of *Schefflera morototoni* on the study area in central Puerto Rico Feb–May 1998.

	Focal tree visitation (<i>N</i> = 24 trees) ^a		Plot-level observations (<i>N</i> = 26 d)	
	No. of visits (%)	No. of trees (%) ^b	No. of obs. (%)	No. of days (%) ^c
<i>Spindalis portoricensis</i>	382 (86.2)	23 (95.8)	45(68.2)	18 (69.2)
<i>Vireo altiloquus</i>	25 (5.6)	10 (41.7)	3 (4.5)	3 (11.5)
<i>Turdus plumbeus</i>	9 (2.0)	2 (8.3)	0 (0.0)	0 (0.0)
<i>Nesospingus speculiferus</i>	8 (1.8)	5 (20.8)	4 (6.1)	2 (7.7)
<i>Melanerpes portoricensis</i>	7 (1.6)	3 (12.5)	0 (0.0)	0 (0.0)
<i>Columba squamosa</i>	4 (0.9)	2 (8.3)	5 (7.6)	3 (11.5)
<i>Myarchis antillarum</i>	3 (0.7)	3 (12.5)	0 (0.0)	0 (0.0)
<i>Margarops fuscatus</i>	2 (0.5)	2 (8.3)	1 (1.5)	1 (3.8)
<i>Contopis portoricensis</i>	2 (0.5)	1 (4.2)	0 (0.0)	0 (0.0)
<i>Tyrannus caudifasciatus</i>	1 (0.2)	1 (4.2)	1 (1.5)	1 (3.8)
<i>Tyrannus dominicensis</i>	* (0.0)	* *	4 (6.1)	3 (11.5)
<i>Loxigilla portoricensis</i>	* (0.0)	* *	1 (1.5)	1 (3.8)
<i>Euphonia musica</i>	* (0.0)	* *	1 (1.5)	1 (3.8)
<i>Dendroica tigrina</i>	* (0.0)	* *	1 (1.5)	1 (3.8)

^a* = Species observed visiting focal trees but known not to have consumed fruit.

^bNumbers in parentheses refer to the percentage of the 24 focal trees visited; thus, they do not sum to 100%.

^cNumbers in parentheses refer to the percentage of the 26 d on which observations were recorded; thus, they do not sum to 100%.

Alchornea latifolia, which occurred in fewer than five neighborhoods. Focal tree crop sizes were relatively large, and conspecific fruits were typically much more abundant than heterospecific fruits in fruit neighborhoods (Fig. 2). *Spindalis portoricensis* visitation and total visitation were influenced by both crop size and neighborhood variables (Table 2). Visitation was positively related to focal tree fruit abundance (although this vari-

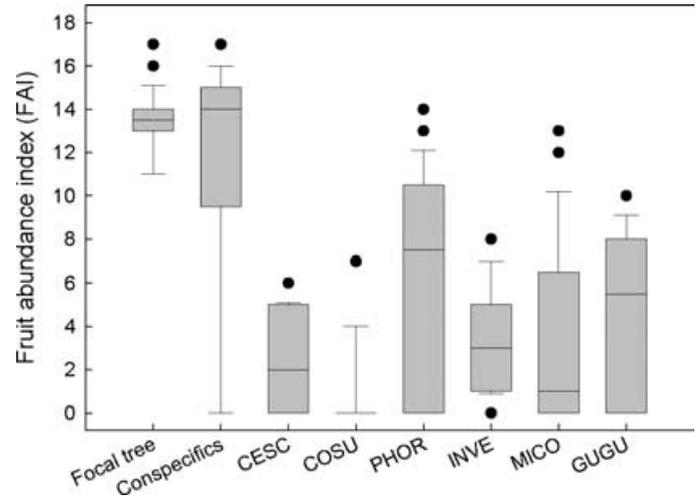


FIGURE 2. Box plots representing focal tree ripe fruit abundance and the abundance of ripe fruits in neighborhoods surrounding focal trees on the study area in central Puerto Rico. See Figure 1 for species code definitions; only species with at least plot-level frugivory observations and present in at least five neighborhoods are shown. Fruit abundance was categorized using an index (the FAI), which essentially followed a log₂-scale (0 = no ripe, 1 = 1–16 ripe, 2 = 17–32 ripe, 3 = 33–64 ripe, . . . , 16 = 262,145–524,288, 17 = > 524,288). Horizontal lines show medians. Boxes span the first through third quartiles (note: the first three quartiles = 0 for COSU), whiskers span the 10–90 percent range, and dots show outliers.

able was only significant in the neighborhood P–A model describing total visitation) and negatively related to the presence or abundance of conspecific fruits. The presence or abundance of heterospecific fruit taxa had mixed effects on visitation. Two taxa, *G. guidonia* and *Phoradendron* spp., were negatively related to at least one response variable, while three others, *Cecropia schreberiana*, *C. sulcata*, and *Inga vera*, were positively related to at least one response variable.

TABLE 2. Results of multiple regressions modeling visitation to 24 *Schefflera morototoni* trees on the study area in central Puerto Rico as a function of crop size and fruit neighborhood variables. Models were selected using a backward stepwise procedure with probability to remove a variable = 0.1

Variable	<i>Spindalis portoricensis</i> visitation				Total visitation			
	Neighborhood P–A Model		Neighborhood FAI Model		Neighborhood P–A Model		Neighborhood FAI Model	
	Standard coefficient	<i>P</i> -value	Standard coefficient	<i>P</i> -value	Standard coefficient	<i>P</i> -value	Standard coefficient	<i>P</i> -value
Focal tree FAI	0.63	0.10			1.20	<0.05		
Conspecifics	−0.77	<0.05	−0.68	<0.05	−0.90	<0.05	−0.69	0.06
Heterospecifics								
<i>Cecropia schreberiana</i>	0.81	<0.05			0.89	<0.05		
<i>Cordia sulcata</i>	0.61	0.10						
<i>Phoradendron</i> spp.	−0.89	<0.05	−1.11	<0.01			−1.01	<0.01
<i>Inga vera</i>			1.20	<0.001			1.37	<0.001
<i>Guarea guidonia</i>					−1.03	<0.05		
	<i>R</i> ² = 0.54		<i>R</i> ² = 0.59		<i>R</i> ² = 0.48		<i>R</i> ² = 0.54	

Selected regression models explained about half the variation in visitation response variables. Neighborhood FAI and neighborhood P–A models differed with respect to which heterospecific fruit taxa were retained. Neighborhood FAI models explained more variation in visitation than neighborhood P–A models, and this larger amount of variation was explained with fewer variables. Selected neighborhood P–A models differed in which heterospecifics showed statistically significant influences on visitation; however, the simpler model (for total visitation) had nearly as strong support as the selected one for *S. portoricensis* visitation ($R^2 = 0.47$ for both). In most regression models, neighborhood variables had larger effects on visitation than crop size.

DISCUSSION

Our regression models suggested that frugivore visitation rate was affected by crop size and neighborhood variables. Visitation rate was positively related to focal tree ripe fruit abundance and negatively related to the presence or abundance of nearby conspecific fruits. Relationships between focal tree visitation and heterospecific fruits were varied—some taxa were positively related and others negatively related to focal tree visitation. These findings suggest that both competition for dispersers (intra- and inter-specific) and facilitation among plants played roles in affecting patterns of bird visitation to focal trees. Although competition among plants has long been a central theme in studies of fruiting plant–frugivore systems (McKey 1975, Howe & Estabrook 1977), few studies report facilitative interactions (Sargent 1990, García *et al.* 2001, van Ommeren & Whitham 2002). Furthermore, interspecific plant–plant interactions (either competitive or facilitative) have rarely been reported for fruiting plant–frugivore systems (Herrera 1984, García *et al.* 2001, van Ommeren & Whitham 2002), despite many such studies in other plant–animal consumer systems (*e.g.*, for pollination: Feinsinger *et al.* 1986; for herbivory: Hambäck *et al.* 2000, White & Whitham 2000).

The strength and direction of interactions among plants that share seed-dispersing frugivores could depend on a variety of factors. The relative availability of various fruit types, which depends on the distributions, sizes, and phenologies of plants, is likely of particular importance. In our study, the most abundant neighborhood fruits (*i.e.*, those of conspecifics and, to a lesser degree, of *Phoradendron* spp. and *Guarea guidonia*) were the ones that appeared to compete with focal trees for frugivores. Fruit types that were relatively rare, on the other hand, seemed to facilitate (enhance) visitation to focal trees. The rarity and patchiness of two of these, *Cordia sulcata* and *Cecropia schreberiana*, resulted, in part, from their nearing the end of their fruiting periods (Carlo *et al.* 2003), and it is possible that their positive (albeit nonsignificant for *Cordia*) relationships with focal tree visitation stemmed from birds switching from these declining and rare resources to nearby abundant *S. morototoni* fruits. Indeed, the principal frugivore in our study, *S. portoricensis*, does seem to concentrate foraging in the same local (neighborhood scale) areas despite changing fruit species composition in those areas (Saracco *et al.* 2004). Although *Inga vera* fruits were more abundant and evenly distributed than *Cordia* and *Cecropia*, *I. vera* also produces abundant nectar and flowers that are consumed by frugivores. Thus, it is possible that birds were responding more to patterns in the availability of *I. vera* flowers than to patterns in the abundance of *I. vera* fruits.

Chemical and nutrient relationships between focal tree fruits and neighborhood fruits could have also affected the ways in which they interacted for seed-dispersing frugivores (Izhaki & Safriel 1989, Cipollini & Levey 1997). For example, conspecific fruits are very similar chemically (and thus “substitutable”; *sensu* Schmidt *et al.* 1997) and should thus compete with one another whenever seed dispersers are a limiting resource. *Schefflera morototoni* seed dispersers were clearly a limiting resource in our study, as their fruits were extraordinarily abundant and most fruits failed to be removed. Although we lack data on the chemical composition of fruits in our study site, fruits of both species with significant positive relationships with focal tree visitation, *C. schreberiana* and *I. vera*, are sugary (see Herbst 1986 for *Cecropia* macronutrient data in Costa Rica) and may have been nutritional complements to the more lipid- and protein-rich fruits of *S. morototoni* (Snow 1971, Herrera 1981). Such complementarity may be common among bird-consumed fruits (Whelan *et al.* 1998), and is supported by the variety of studies that report dietary mixing in frugivorous birds (Loiselle 1990, White & Stiles 1990, Blake & Loiselle 1992, Poulin *et al.* 1999).

Differences between neighborhood FAI and P–A models in which heterospecific fruit taxa were retained by the backward stepwise regression procedure probably resulted from differences in the distributions and abundances of the various fruit taxa. The most abundant (*Phoradendron* spp.) and the least skewed (*I. vera*) taxa (*i.e.*, the ones with the best representation over a range of values) were the only ones included as FAI variables. In contrast, the least abundant and highly right-skewed taxa (*Cecropia* and *Cordia*) were only included as P–A variables. Because these fruits were uncommon and patchily distributed, frugivores may have been more likely to respond to their presence than their abundance.

Finally, differences between response variables in which heterospecific fruit taxa were retained in neighborhood P–A models likely reflected differences in fruit preferences between *S. portoricensis* and other *S. morototoni* consumers. Specifically, *C. sulcata* was exclusively consumed by *S. portoricensis*, and as such, was only retained as an explanatory variable in the *S. portoricensis* visitation model. *G. guidonia*, which was mostly consumed by the second most common focal tree visitor, *Vireo altiloquus* (Carlo *et al.* 2003), was only included in the total visitation neighborhood P–A model.

CONCLUSIONS

The high variability seemingly inherent in most fruiting plant–frugivore systems has led many researchers to question the notion that frugivores exert strong selection pressure on individual plants, and ultimately on the coevolution of fruiting plant–frugivore mutualisms (Howe 1984, Wheelwright 1991). Our results suggest that interactions among neighboring plants are important elements driving variation in frugivory among plants that share avian seed-dispersers. Future studies aimed at demonstrating the nature and consistency of these types of interactions at various spatial and temporal scales should provide a broader understanding of the relative importance of various levels of selection (*i.e.*, individual, population, and community) in the evolution of zoochorous seed dispersal systems.

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